

Sex ratio in a population of *Lestes viridis*: spatial and temporal variability at emergence (Odonata: Lestidae)

Karl Westermann

Buchenweg 2, 79365 Rheinhausen, Germany. <karl.westermann@googlemail.com>

Key words: Odonata, dragonfly, sex ratio, spatial variability, protogyny, habitat relation, small-scale differences, sample size, *Lestes viridis*.

ABSTRACT

In a large population of *Lestes viridis* inhabiting a complex, extended system of channels in the floodplain of the Upper Rhine River near Weisweil (Baden-Württemberg, Germany) detailed samples of exuviae were collected from several subpopulations. For each sample the sex ratio was determined. For statistical reasons only samples with at least 700 exuviae were considered. These samples sometimes differed highly significant in the sex ratio at emergence. The sex ratio was site-specific, but differed significantly for different subpopulations with variation in water temperature. Thus, damselfly larvae showed sex-dependent habitat preferences. The frequency of males ranged from 49.4% to 57.5%. Statistically significant small-scale differences in sex ratio, which have not previously been described, could not be attributed to different preferences of the sexes with respect to larval habitat and emergence site. No coherent explanation for this phenomenon could be advanced. Females on average emerged earlier than males; in one of the samples the median emergence date differed by four days.

INTRODUCTION

In most Odonata populations, the primary sex ratio is balanced (Lawton 1972; Corbet 2004: 252). However, skewed sex ratios regularly occur at emergence. For Zygoptera, the proportion of males is often greater than for Anisoptera (Corbet & Hoess 1998; Corbet 2004: 252). The mechanisms for the formation of an unbalanced sex ratio, and its function, are not known for any particular cases (Lawton 1972; Corbet 2004: 252). In principal, unbalanced sex ratios of a subpopulation should result from differential mortality of the sexes during the pre-imaginal development or segregation during the larval stadia. It might also reflect female oviposition behaviour – a non-random pattern in sexes of fertilized eggs might occur due to differential sperm motility within the spermatheca (A.G. Orr pers. comm.). Different responses of the sexes in their larval stage (e.g. Baker et al. 1992; De Block & Stoks 2003, 2005) to various habitat factors could cause differential mortality (Baker et al. 1992; Corbet 2004: 252) or differential migration patterns of the larvae.

In most previous studies, only one or a few samples of the sex ratio at emergence in a given population were collected (overview in Corbet & Hoess 1998), so that little is known about its variability. Corbet (2004: 252) points out one example of a varying sex ratio in different years and in different habitats, respectively. In an extreme case, the sex ratio in 18 small and moderately large samples of *Gomphus vulgatissimus* (Linnaeus) from Central Europe ranged from 30.7% to 72.4%. The two extreme values originated from the same study area and differed at a highly significant level from a balanced sex ratio of 50.0% (Müller 1995; Corbet & Hoess 1998). Generally in Odonata, the two sexes emerge at approximately the same time, but differences do occur. So far, cases of protandry rather than of protogyny have been found (Corbet 2004: 250).

Over several years, exuviae were intensively collected along a system of water bodies on the Upper Rhine in Southwest Germany to determine the abundances and dominances of various odonate species (Westermann 2002a). *Lestes viridis* (Vander Linden) was found to be very abundant and was therefore well suited for further investigations (Westermann 2000, 2002b, 2006, and unpubl. data). Intensive studies in 2002 and 2003 aimed to maximise data in order to test previous results of skewed sex ratios in various subpopulations (K. Westermann unpubl.) and of protogyny (Westermann 2002b). Moreover, a possible difference among the sexes with respect to the choice of the emergence habitat was also investigated.

MATERIAL AND METHODS

The study area was situated on the alluvial plains of the river Rhine near the village of Weisweil, Federal State of Baden-Württemberg, Germany (48°12'N, 07°39'E), which is located ca 27 km NW of Freiburg im Breisgau and 43 km S of Strasbourg. At that site, there was a complex, extended backwater system of the channelized Rhine. The investigations were conducted along different sampling stretches of the "Altrhein" and at its tributary "Hexenkehle" (Fig. 1). In the study area, the Altrhein was ca 32-40 m wide and featured predominantly eutrophic water that originated from the Rhine. At normal flow conditions, the maximum rate of flow ranged from 0.1 to 0.2 m/s, and the maximum depth between 1.0 and 2.2 m. Except for flooding periods, the Hexenkehle was fed exclusively by weak springs. With a width between 11 and 24 m and maximum depths ranging from 0.8 to 2.2 m, water flow was scarcely discernible. At normal air temperatures, the water temperatures in summer ranged from 14-16°C in the upper course to 19-21°C in the lower course (Westermann & Westermann 1998; Westermann 2002a). Both waters were surrounded by dense forests of the former floodplain.

On all sampling stretches, exuviae were collected from a kayak, which significantly increased the accuracy and reduced damage to the vegetation and the emerging imagines.

Sample site A: A 46 m long section of bank of the Altrhein (Fig. 1). During the emergence season of 2002, if possible, all visible exuviae of *Lestes viridis* were collected daily for 6-10 hours. The emergence began on 4 July; collection of exuviae started on that date and was conducted daily, independent of weather conditions, from 5 July to 2 August. Sampling was concluded on 5 and 14 August with the search for the few "stragglers". Mostly, I began sampling at ca 09:30 h solar time, when individuals had

broadly finished their emergence and insignificant damage was done to them during sampling. Through repeated inspections of the sampling stretch, imagines that had emerged late on that day could be detected with their exuviae.

For each exuvia, the sex was determined, and its location was measured to an accuracy of 0.1 m using surveying poles with a 2.0 m spacing. To investigate potential sex-specific preferences in the emergence habitat, various habitat factors were recorded for each exuvia (see below). However, for logistic reasons, it was often impossible to obtain a complete data set. Owing to the long period spent in observation at the study site and the clearly defined, relatively homogenous vegetation on the bank, a high level of accuracy could be achieved. At the water's edge, *Phalaris arundinacea* dominated, with *Carex acutiformis*, *C. elata* and sparse stocks of *Phragmites australis* occurring frequently. Among the conceivable aquatic habitat parameters of the Altrhein along the sampling stretch, there was a dense growth of *Elodea nuttallii* close to the shore that was at least 2 m wide and reached the surface. Further aquatic habitat parameters were the other macrophyte vegetation, the water depth and the flow velocity. All these features proved to be relatively uniform throughout the sampling stretch.

On the same sampling stretch, I had previously collected all exuviae within reach during the entire emergence period from 1999 to 2001 and determined the sex ratio (cf. Westermann 2002b). These results were used for comparison.

Sample site B: 1999-2001; four pillars of a ca 40 m wide bridge across the Altrhein. Only parts of the two outer pillars reached the water (Fig. 1; details in Westermann 2003).

Sample site C: A ca 95 m long shore area at the upper course of the Hexenkehle (Figs 1, 4); maximum linear distance to sampling stretch A 800 m.

Here, I collected exuviae and determined the sex ratio of *L. viridis* every 2-3 d during the very hot summer of 2003. Rain events which may cause a loss of exuviae did not occur during the study time. During the summer, *Sparganium emersum* occupied areas of 0.5-30 m² and developed leaves above the water surface, where a large percentage of *L. viridis* emerged. Other emergence substrates occurring at lower frequencies included emergent woody debris as well as *Carex* spp. and *P. arundinacea* near the water's edge. Thus, the differences in the emergence substrates were minor. In this and other years, the emergence period was delayed by several weeks compared with the Altrhein (Westermann 2002b).

On this sampling stretch, I had previously collected all accessible exuviae during the entire emergence periods of 1999 and 2000 and determined the sex ratio; 1999 experienced a major flood event with long-lasting high water levels from mid May until mid July, which initially even exceeded long-term maximum values. The year 2000 could be classified a "normal year" with respect to water levels and weather conditions (cf. Westermann 2002b). The results were used to compare the sex ratios realised under different external conditions.

Sample sites D-G: Stretches of the Hexenkehle (D-F) and a small, strongly shaded side channel (G), respectively (Fig. 1). Particularly in the "flood year" 1999, the exuviae were systematically collected and the sex ratio was determined (cf. Westermann 2002b). The data were used for a comparison with those of the sampling stretches A and C.

Sample site H: Altrhein between the mouth of the Hexenkehle and the bridge B (Fig. 1). In late summer and autumn 1999 and 2000 I looked for the oviposition sites of *L. viridis* to prepare a study on the oviposition substrates (Westermann 2000). By these, I gained important information on the migration of larvae from the lower Hexenkehle to the Altrhein. Following a massive eutrophication during the flood in 1999, the macrophyte populations in the lower Hexenkehle almost entirely died off, so that there was virtually no physical protection for dragonfly larvae and presumably also their prey had largely vanished. Accordingly, the populations of all dragonfly species strongly decreased from 2000 onwards. — The sample site A was a short subsection of H.

Statistical analysis

The following procedures were used:

- χ^2 -tests in contingency tables for the comparison of the ratios of the two sexes, for the comparison of two medians and to check the homogeneity of the sex ratio of a sampling stretch and of habitat factors of the emergence site, respectively;
- Spearman's rank correlation, calculation of a regression line;
- calculation of the standard error of the sex ratios of the samples to determine the 95% confidence interval;
- z-test to compare the mean values of single habitat factors of the emergence location for the two sexes.

Terminology

The 'biological population' was defined as the population of the alluvial floodplain of Weisweil. Apart from the subpopulations studied, it comprised a number of additional subpopulations.

All samples, whose sex ratios did not differ statistically significantly, originated from the same 'statistical population' with respect to their sex ratio (cf. Fowler et al. 1998).

As usual, the proportion of males in the total number of imagines, which emerged during the emergence period, was defined as 'sex ratio g'.

The investigations of emergence provided samples for estimating the sex ratio. For each sampling site these data were influenced by practical considerations, dependent for example on year, type of habitat or perhaps even the state of the weather, water level or current flow. For each sample, the sex ratio of the respective statistical population – not to be confused with the much wider biological population – was estimated within a confidence interval. Since the width of the confidence interval increases with decreasing error probability and decreasing size of the sample, 95% confidence intervals were used in this work and only samples of at least 700 exuviae were considered. In the case of sex ratios around unity, a single sample with 100 or a few 100 exuviae provided a confidence interval between 10 and 20%. Hence, it only allowed for crude results, which were to be expected according to general experience. Very large samples could be divided in classes of sex ratios of a day or a subsection, even if a few outliers had to be thereby accepted.

Only in very few cases, was the sex of the exuviae accidentally not determined.

RESULTS

Changes of the sex ratio during the course of the emergence season

In 2002, at the sample site A of the Altrhein, the sex ratio slowly shifted throughout the emergence season towards males. Despite a few outliers, the correlation was highly significant (Spearman's rank correlation $r_s = 0.681$, $n = 22$, $u = 3.12$, $p < 0.005$, two-tailed test). Every five days, the sex ratio on average changed by ca 3% (Fig. 2).

The medians of the male and female emergences curves most strikingly demonstrated the differences of the sexes: for the females the median fell on 16 July, for the males on 20 July. A simple median test yielded a highly significant difference (Tab. 1).

Females also once again dominated among the last few imagines, to emerge. Out of the last nine individuals, eight were females, and among the last 30, 20 were females. However, due to the small sample sizes, this was not a statistically significant result.

At sampling site C of the upper Hexenkehle, where emergence was delayed by several weeks compared with the Altrhein in 1999 and 2000, more females also emerged at the beginning of the emergence season in 2003. After ca 10 days, no more differences were found. The medians of the two sexes differed only marginally. During the period from 10 July to 17 July g was found to be 45.7% ($n = 339$), and from 19 July to 19 August to be 57.8% ($n = 3,858$). The difference in sex ratio between the two periods was statistically highly significant ($\chi^2 = 18.6$; $p < 0.001$).

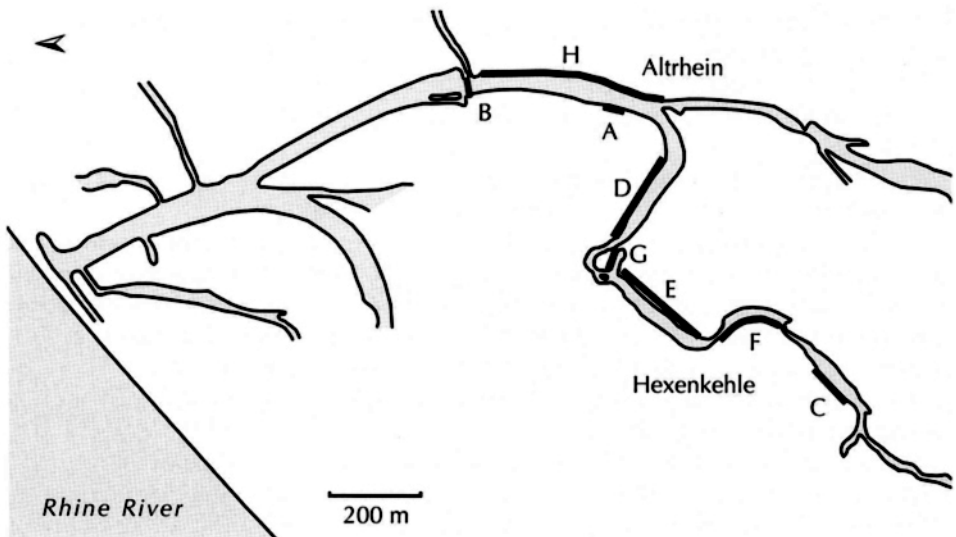


Figure 1: Emergence sites of *Lestes viridis* — map of the sample sites A-H in the floodplain of the Upper Rhine River. Both banks are included in D, G and H but, for simplicity, only one bank is figured.

Table 1. Number of newly emerged individuals of *Lestes viridis* at sample site A before and after the median of female emergence on 16 July ($\chi^2 = 21.7$, $p < 0.001$).

	Males	Females
Emergence before 16 July	772	888
Emergence after 16 July	1,057	890

Table 2. Emergence data of *Lestes viridis* in 1999-2001 at sample site D of the Hexenkehle and sites A, B and H of the Altrhein, from which a migration of larvae from D to A is concluded. A and B are small subsections of H; cf. Figure 1 and text.

Sample site	Number/abundance	1999	2000	2001
D	Exuviae (subsection)	3,357	95-100	269
	Ovipositions	Very frequently	Very rare	-
A	Exuviae	18	1,832	1,794
B	Exuviae	4	56	836
H	Ovipositions	Very rare	Frequently	-

Table 3. Number N of groups with sample size n , for which the sex ratio of *Lestes viridis* was independently calculated at sample site A in 2002. See text.

n	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-178
N	5	21	8	6	5	4	5	3	4	7

Table 4. Sample size n and sex ratio g [%] of *Lestes viridis* at the subareas 1-12 of sample site C in 2003 (Fig. 4). Error probability is given for comparisons between the subareas.

	1	2	3	4	5	6	7	8	9	10	11	12
n	168	139	109	653	356	1,014	128	304	527	163	294	267
g	64.3	61.9	61.5	60.5	58.4	58.0	57.8	55.6	54.6	54.6	51.0	50.6
1	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.01	0.005
2	-	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	< 0.05	< 0.05
3	-	-	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	< 0.01	n.s.
4	-	-	-	-	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.01	< 0.01
5	-	-	-	-	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.05
6	-	-	-	-	-	-	n.s.	n.s.	n.s.	n.s.	< 0.05	< 0.05
7	-	-	-	-	-	-	-	n.s.	n.s.	n.s.	n.s.	n.s.
8	-	-	-	-	-	-	-	-	n.s.	n.s.	n.s.	n.s.
9	-	-	-	-	-	-	-	-	-	n.s.	n.s.	n.s.
10	-	-	-	-	-	-	-	-	-	-	n.s.	n.s.
11	-	-	-	-	-	-	-	-	-	-	-	n.s.
12	-	-	-	-	-	-	-	-	-	-	-	-

Site-specific differences in sex ratio

Sample site A: In 2002, the total of collected exuviae ($n = 3,706$; 1,871 ♂, 1,835 ♀, 10 sex not identified) yielded a sex ratio of $g = 50.5\% \pm 1.6\%$. For comparison, the sex ratio was $g = 49.4\% \pm 2.3\%$ ($n = 1,792$) in 2001. The two values did not differ significantly ($p > 0.40$), and hence originated from the same statistical population. Thus, the two samples could be merged to a single sample with $g = 50.1\% \pm 1.3\%$ ($n = 5,498$). Neither of the two samples differed significantly from a sex ratio of 50.0%.

Unusual conditions in 2000 led to a slightly different sex ratio. According to the number of exuviae in 1999, oviposition occurred extremely frequently in September and October of the same year at the lower Hexenkehle (sampling stretch D), whereas it was rare at the Altrhein (sampling stretch H with the shorter subsection A) – for each control, a maximum of five pairs along 400 m of shoreline was recorded. In stark contrast, an extremely large number of imagines emerged at H in the following year 2000, while only few emerged at D. The number of exuviae increased by a factor of 100 compared with 1999 at sampling site A (Tab. 2), which is situated close to the mouth of the Hexenkehle. Obviously, a large number of the larvae from the by then devastated lower Hexenkehle (see p. 118) had migrated to the adjacent Altrhein. At sample site B of the Altrhein, which was situated at least 300 m downstream, the increase in the number of exuviae in 2000 was found to be much smaller, but the numbers continued to increase in 2001 (Tab. 2). — In 2000, the sex ratio at the sampling stretch A with $g = 52.6\% \pm 2.3\%$ ($n = 1,832$) remained higher than in the two following years. The statistical significance compared with the value of 2001 was only just rejected ($\chi^2 = 3.79$; $p = 0.052$). In 1999, a very similar value of $53.1\% \pm 1.1\%$ was determined at the sampling stretch D, from where the larvae originated (see below).

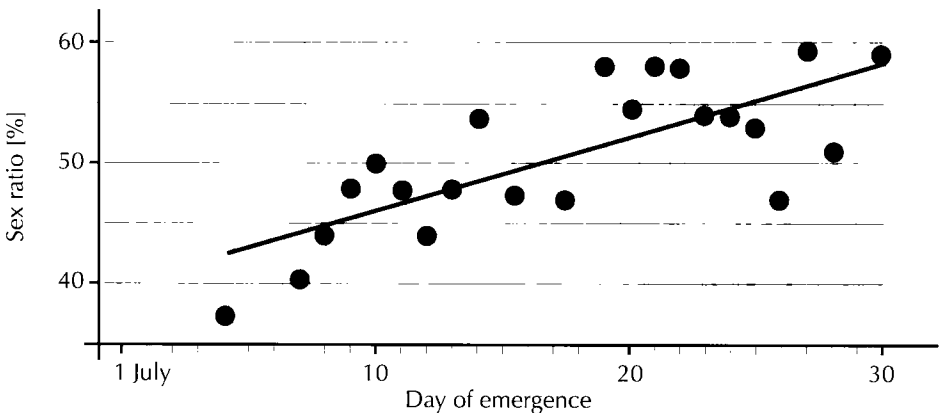


Figure 2: Sex ratio g of *Lestes viridis* at the sample site A in 2002 in relation to the day of emergence. If the sample size was < 100 , the samples from consecutive days were lumped and attributed to the medium date. Sex ratio $g = (0.597 \times E + 39.54)\%$; $R^2 = 0.562$. E : day of emergence, consecutive number of days starting at 1 July.

Sample site C: In the “hot year” 2003, the sex ratio was found to be $g = 56.9\% \pm 1.5\%$ ($n = 4,197$). The difference from site A (2002) was highly significant ($\chi^2 = 32.6$, $p < 0.001$). Hence, the two samples did not belong to the same statistical population. In the “flood year” 1999, g was $57.5\% \pm 1.5\%$ ($n = 3,964$) and in the “normal year” 2000, g was $55.5\% \pm 1.5\%$ ($n = 4,475$). The three values from sample site C do not differ significantly ($p > 0.10$), and thus originate from the same statistical population. Furthermore, there was no significant difference between the two samples with the highest and the lowest sex ratio ($\chi^2 = 3.37$, $p > 0.05$). Hence, all three samples could be merged to a single sample with a sex ratio of $g = 56.6\% \pm 0.9\%$ ($n = 12,636$). All three samples differed with a high level of significance ($p < 0.001$) from a sex ratio of 50.0%.

Sample sites D-G: In 1999, the sex ratio at site D was $g = 53.1\% \pm 1.1\%$ ($n = 7,666$), at site E $g = 52.9\% \pm 1.3\%$ ($n = 6,031$) and at site F $g = 53.3\% \pm 1.9\%$ ($n = 2,635$). At site G, g was $54.3\% \pm 3.7\%$ ($n = 700$) in 1999 and $53.7\% \pm 3.2\%$ ($n = 929$) in 2001. There were no significant differences between the sites D-G. All samples were merged and yielded a sex ratio of $g = 53.1\% \pm 0.7\%$. These merged samples showed a highly significant difference from those of the two other areas ($\chi^2 = 11.84$ and 35.50 , respectively; $p < 0.001$). Hence, the samples from the three sampling stretches A, D-G and C belong to different statistical populations.

The three samples from D, E and F and the merged samples from G from the two years differed with high statistical significance ($p < 0.001$) or statistical significance ($p < 0.05$) from a sex ratio of 50.0%.

Small-scale differences in the sex ratio

Sample site A (2002): First, the sex ratios were calculated independently for all subsections of 0.1 m length, and then merged with consecutive subsections with ‘similar’ values or generally with small numbers ($n < 11$). In this way, 68 groups were formed, of which 55 had shore lengths between 0.1 and 1.0 m, 11 had shore lengths between 1.1 and 2.0 m and two had shore lengths of 3.1 m each. The long lengths were mostly due to subsections with small abundances. An overview of the sample sizes n of the 68 groups is given in Table 3.

The distribution was extremely heterogeneous (Fig. 3; $\chi^2 = 200.2$, d.f. = 67, $p < 0.001$, threshold value for $p < 0.001$ at ca 112). High sex ratios were e.g. 14 ♂, 1 ♀ – 18 ♂, 5 ♀ – 20 ♂, 8 ♀ – 40 ♂, 17 ♀ – 52 ♂, 27 ♀ – 60 ♂, 32 ♀, and low sex ratios 9 ♂, 24 ♀ – 25 ♂, 48 ♀ – 30 ♂, 58 ♀, respectively. For single days, a corresponding effect could not be proven even for the highest densities of exuviae of 210 to 250 exuviae per day and 46 m length.

Sample site C (2003): In the field, 25 different subareas were distinguished. Adjacent areas with similar sex ratios were then merged to 12 groups, which were better suited for a statistical analysis due to the larger sizes of the samples (Fig. 4). Ca 74% of the individuals emerged in the *Sparganium* vegetation off the bank, the rest on the bank. The sex ratios of the 12 samples were significantly heterogeneous ($\chi^2 = 20.44$, d.f. = 11, $p < 0.05$). Furthermore, the sex ratios of single subareas showed a significant or highly significant difference (Table 4).

Table 5. Tested habitat preferences of the sexes of *Lestes viridis* at emergence. z-Test for mean values; *n*: number of measured locations of exuviae; *H*: height of the emergence location above the water surface; *D*: distance of the emergence location from open water; *W*: water depth at the emergence location.

Factor	Mean/standard deviation		<i>n</i>	<i>z</i>
	Males	Females		
<i>H</i>	(33.5 ± 24.3) cm	(33.0 ± 23.3) cm	3,520	0.65 (n.s.)
<i>D</i>	(56.9 ± 28.5) cm	(57.4 ± 28.3) cm	3,468	0.52 (n.s.)
<i>W</i>	(13.8 ± 7.9) cm	(14.0 ± 8.1) cm	2,798	0.66 (n.s.)

Habitat factors and sex ratio

The influence of habitat factors on the sex ratio was investigated at sample site A. The imagines emerged almost exclusively on the shore vegetation above shallow water. The mean value of the height of the emergence location above the water surface, its distance from the open water and the water depth at the emergence location did not differ significantly for the two sexes (Table 5). No heterogeneity between the sexes was found for the following habitat factors:

- angle between emergence support and exuvia
- structure of the emergence support (leaf, stem, etc.)
- plant species
- position (below or to the side) of the emergence site with respect to the emergence support
- degree of vegetation cover surrounding the emergence site (Table 6)

Additional habitat factors, such as the proportion of shade, the canopy of branches of deciduous trees and the existence of small inlets, varied over a much greater range than the sex ratio. The water temperature at a given time was constant throughout the entire sampling stretch and changed only marginally during the emergence season.

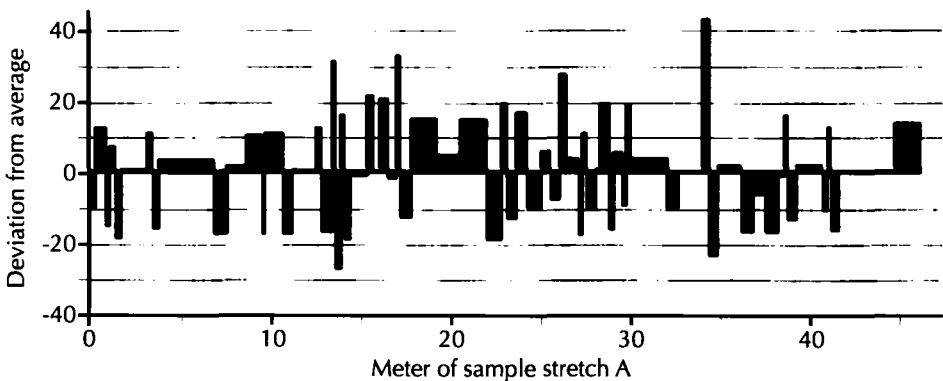


Figure 3: Deviation of the sex ratio of *Lestes viridis* from the average value of 50.5% at sampling stretch A in 2002. Sixty-eight groups along shore lengths from 0.1 to 3.1 m; cf. Table 3 and text.

Table 6. Tested habitat preferences of the sexes of *Lestes viridis* during emergence for several habitat factors. A: angle between emergence support and exuvia (cf. Westermann 2006); S: structure of the emergence support: stem leaf, stem, terminal leaf/flower; Sp: plant species – classified as *Carex acutiformis*, *C. elata*, *Phalaris arundinacea*, *Phragmites australis* and others; P: position of the emergence site with respect to the emergence support, below or to the side; C: degree of vegetation cover (five classes) in ≤ 30 cm distance from the emergence site; N: number of classes for each sex.

Factor	n	N	d.f.	χ^2
A	3,498	10	9	12.3 (n.s.)
S	3,470	3	2	1.10 (n.s.)
Sp	3,597	5	4	5.99 (n.s.)
P	3,466	2	1	0.55 (n.s.)
C	2,769	4	3	0.65 (n.s.)

At sample site C, the habitat characteristics of the emergence sites were largely identical for $\frac{3}{4}$ of the exuviae. The water temperature did not change at such small scales, as the sex ratio did.

Hence, no sex-specific differences with respect to any factors of the emergence habitat were detected.

DISCUSSION

Changes of the sex ratio during the course of the emergence season

At sample site A of the Altrhein in 2002, the proportion of males of *Lestes viridis* continuously increased more or less throughout the entire emergence period (Fig. 2). Hence, protogyny is proven in this example. Along sample site C of the upper Hexenkehle in 2003, significant differences compared with site A were found, since females dominated only at the beginning of the emergence period, quickly followed by a constant sex ratio with a strong dominance of males. Thus, at the upper Hexenkehle, the males emerged earlier relative to the females than on the sampling stretch A of the Altrhein. This may have been triggered by the lower water temperatures, which led to a delayed emergence (Westermann 2002b) and hence probably to time constraints for development at the upper Hexenkehle. However, it is not feasible to directly compare the years 2002 and 2003. In the “hot year” 2003, the species emerged up to three weeks earlier than usual throughout the entire study area, with differences between the subpopulations at the Altrhein and the upper Hexenkehle remaining consistent (K. Westermann unpubl.). Previous less detailed samples from both the Altrhein and the Hexenkehle show a significantly increasing proportion of males until the median (Westermann 2002b).

In a large sample of *L. viridis*, the prolarvae emerged over a period of six weeks, with the females emerging on average three days earlier than the males with a high level of statistical significance (De Block & Stoks 2005). Under laboratory conditions and in an insectary, respectively, males on average needed less time for development than females (De Block & Stoks 2003, 2005), which at least partially com-

pensates for the lag of the males due to the emergence of the prolarvae. This example and the examples from wild populations presented here suggest, that the proven protogyny is specific for the species *L. viridis*, but can vary according to ecological conditions. In the case of *Anax imperator* (Leach), Corbet (1957) found in different years either protandry, protogyny or simultaneous emergence of the sexes at the same water body. — Along sampling stretch A, the lag of the males due to the later emergence of the prolarvae (De Block & Stoks 2005) may have persisted on average, since no larval constraints should have occurred due to the earlier emergence and a presumably good food supply.

Another European example for protogyny was found for *Coenagrion puella* (Linnaeus) in northern England. There, the emergence of females on average occurred statistically significantly 1.4 days earlier than the emergence of the males. The pre-reproductive period for females is on average three days longer than for males, which could enhance selection in favour of earlier emergence by females (Thompson 1989). To my knowledge, no quantitative data on the average duration of the prereproductive period of the sexes exist for *L. viridis*, so the function of protogyny (cf. Corbet 2004: 250) can only be a matter of speculation.

Site-specific differences in the sex ratio

The sex ratios at different sample sites differed significantly, although they were situated in the same landscape and at the same, continuously populated system of waters at a linear distance of no more than 800 m from each other. Obviously, the two sexes had different larval habitat preferences. The following minimum conditions for a proof were fulfilled:

- (1) the differences of the sex ratios from different sites were statistically significant;
- (2) the differences of the sex ratios were site-specific, i.e. proven for at least two different waters or sections of waters each for at least two different years, furthermore under different weather and discharge conditions;

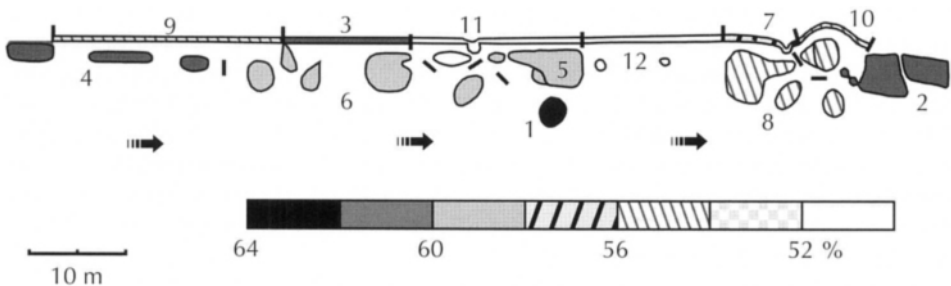


Figure 4: Site map showing the distribution of the sex ratios of *Lestes viridis* at sample site C in 2003. The location and the approximate outline of the twelve subareas with the clumps of *Sparganium emersum* beyond the banks are drawn to scale. Scale of the sex ratio in intervals of 2%. Arrow: direction of the very weak flow of water.

- (3) the water temperature during summer, has been proven to be an environmental factor influencing larval development (De Block & Stoks 2003), and varies over the investigated stretches. The percentage of females in the samples from stretch A over stretches D-G to stretch C decreased along with the decreasing water temperatures. Thus, it is possible that the differences in sex ratio are caused by different water temperatures;
- (4) with a high probability, the subpopulations of the different sampling stretches belonged to the same population, within which genetic differences, that could cause the differences in sex ratio, are not likely.

Furthermore, the Hexenkehle in contrast to the Altrhein is largely a standing water body. The rate of flow could theoretically explain differences between the sampling stretch A of the Altrhein and the stretches C-G of the Hexenkehle, but not the differences within the Hexenkehle between the sampling stretches D-G on the one hand and C on the other hand. Therefore, water current must be discarded as a relevant habitat parameter.

It is not known, what might have caused the differences of the sex ratios of *L. viridis*. It has only been proven that the emergence at the upper Hexenkehle with its relatively low water temperatures during summer is delayed by several weeks compared with the Altrhein (Westermann 2002b). Hence, a longer larval development is to be expected along the sampling stretch C, as was proven under laboratory conditions at cool water temperatures by Pickup & Thompson (1984) for *Lestes sponsa* (Hansemann), and by De Block & Stoks (2003) for *L. viridis*. Nutritional constraints as a different possible cause of the delay (Pickup & Thompson 1984; De Block & Stoks 2005) are not likely due to the high abundances along this stretch (Westermann 2002a, this work). In any case, the reproductive period is shortened for individuals that emerged along stretch C.

Only laboratory experiments can clarify whether differences in behaviour of the sexes lead to an enhanced migration of females away from sections with cool water in summer, or whether the mortality of the larvae is different for the sexes here (Corbet 1962: 252; Jödicke 1997: 177f; Corbet & Hoess 1998). Since at the water adult females, unlike adult males, immediately find a mating partner (Dreyer 1978; own obs.), females might preferably migrate away from sections with cool water in summer, thus reducing time constraints during larval development, which would ultimately increase their lifetime mating success. This would decrease the costs for the females in the larval stage and thus increase their fitness.

An example of migration of larvae is described in the present work: along sampling stretch A, the sex ratio of *L. viridis* in 2000 deviated from the site-specific value and was approximately similar to the sex ratio, that was found in 1999 at sampling stretch D from where the larvae originated; obviously, a large migration of larvae had occurred (see above). In a second case, *L. viridis* emerged in large numbers at a section of a ditch, that was not surrounded by bushes or trees and had for the first time contained water in late autumn of the previous year – the larvae must have migrated to this stretch from sections upstream, presumably along the gradient of increasing water temperatures (K. Westermann unpubl.).

Corbet (2004: 252) interpreted Pajunen's (1962) data on the sex ratio of *Leucorrhinia dubia* (Vander Linden), which contrasts sexual emergence patterns at two neighbouring waters in two consecutive years, as proof of a habitat determined sex

ratio. However, this interpretation must be rejected for several reasons: (1) The sex ratios of the two studied waters did not differ statistically significantly. (2) The sex ratio was not specific for the site. While the habitat factors did not change at the two waters (Pajunen 1962), the proportion of the sex ratios switched from 44.5% : 48.8% in one year to almost the reciprocal value of 48.5% : 44.1% in the following year. (3) Pajunen (1962) did not interpret the differences to be caused by any essential habitat factor.

The sex ratio of the biological population of *L. viridis* in the alluvial floodplains of Weisweil cannot be determined even from a large number of samples. However, it is important to distinguish between different statistical populations. Spring waters, which feature cool water in summer, occur far less often than other water bodies, so that the sex ratio of the biological population is most likely closer to unity than to 56%. Published examples for the sex ratio of *L. viridis* are based on small or moderately large samples and do not differ significantly from unity: 52.7% ($n = 385$) in northwestern Spain (Cordero 1988); 54.4% ($n = 228$) in northern Germany (Jahn 1991); 49.4% ($n = 723$) in western Switzerland (Hoess 1993).

Small-scale differences in the sex ratio

Along the sampling stretches A of the Altrhein and C of the Hexenkehle, the distribution of the sexes was significantly heterogeneous (Figs 3, 4; Table 4). Three reasons for the proven differences are conceivable:

- (1) sex-specific preferences within the emergence habitat;
- (2) sex-specific preferences within the larval habitat, at least during the final stadium F;
- (3) differences in behaviour between the sexes, which lead to a partial spatial separation at least in the final stadium F.

Regarding (1) — At site A, none of the examined habitat factors of the emergence site showed any indication of being responsible for the differences in the sex ratio. At site C, the habitat factors of the emergence site were more or less identical for 75% of the exuviae. Thus, the small-scale differences in the sex ratio can most likely not be attributed to factors of the emergence habitat.

Regarding (2) — Along the Altrhein, some larvae were caught and exuviae were frequently found in areas away from the shore, predominantly on two pillars of sampling site B located centrally in the water, and regularly at emergent leaves of *Butomus umbellatus*, at emergent woody debris or at fixed floating rafts of dead plant matter. This proves that at least some of the larvae live away from the banks and migrate towards the shore prior to emergence. The conceivable habitat parameters of the sections of the Altrhein that are away from the shore are relatively uniform (see p. 117). Thus, for sample site A, it seems unlikely, that the larval habitat might also vary on a small scale congruent with the spatial variation in sex ratio during emergence. Corresponding statements are also valid for sampling stretch C, where a large part of the imagines emerged in uniform populations of *Sparganium* located off the bank.

Regarding (3) — If no sex-specific habitat constraints are present, a proximate factor could be a reduced aggression between larvae of the same sex. Such behaviour could lead to a partial segregation of the sexes, with reduction of competition between the sexes as ultimate factor. So far, it can only be speculated upon this, and

laboratory experiments are the only means to prove or reject this hypothesis. Furthermore, one can assume that during the shore-bound migration of the larvae prior to emergence, any segregation of the sexes would be largely cancelled. Thus, an intuitive explanation for the small-scale differences in the sex-ratio, which according to my knowledge has not yet been described in the odonatological literature, cannot be given.

CONCLUSIONS

Within the same biological population, highly significant differences in the sex ratio of *Lestes viridis* during emergence were proven. The results of the spatial variability of the sex ratio are particularly remarkable. On the one hand, despite a large number of samples, it was impossible to determine the sex ratio of the biological population due to the habitat dependence of this ratio, which suggests we perhaps should review the interpretation of many published data on sex ratio in nature. On the other hand, a new phenomenon was found with a clear small-scale variability of the sex ratio of larvae in the final stadium. For both temporal and spatial variability and the proven imbalances of the sex ratio, the causes remain vague. Only the water temperature could be identified as a likely environmental factor, which can influence the sex ratio.

It must be stressed that these results could only be obtained from a detailed collection of very large samples from different subpopulations.

ACKNOWLEDGEMENTS

Andreas Martens and especially Hansruedi Wildermuth crucially contributed to this work with constructive criticism and stimulating discussions. I thank Andreas Martens, Martin Schorr and Hansruedi Wildermuth for their advice and help concerning literature. My son Sebastian Westermann translated the German version of the manuscript to English, and Albert G. Orr finally polished the language.

REFERENCES

- Baker, R.L., M.L.R. Forbes & H.C. Proctor, 1992. Sexual differences in development and behaviour of larval *Ischnura verticalis* (Odonata: Coenagrionidae). Canadian Journal of Zoology 70: 1161-1165.
- Corbet, P.S., 1957. The life-history of the emperor dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). Journal of Animal Ecology 26: 1-69.
- Corbet, P.S., 1962. A biology of dragonflies. Witherby, London.
- Corbet, P.S., 2004. Dragonflies: behaviour and ecology of Odonata. Revised edition. Harley, Martins.
- Corbet, P.S. & R. Hoess, 1998. Sex ratio of Odonata at emergence. International Journal of Odonatology 1: 99-118.
- Cordero, A., 1988. Estudio ecológico de una población de *Lestes viridis* Vander Linden, 1825 (Zygoptera, Lestidae). Limnética 4: 1-8.

- De Block, M. & R. Stoks, 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of Evolutionary Biology* 16: 986-995.
- De Block, M. & R. Stoks, 2005. Fitness effects from egg to reproduction: bridging the life history transition. *Ecology* 86: 185-197.
- Dreyer, W., 1978. Etho-ökologische Untersuchungen an *Lestes viridis* (Vander Linden) (Zygoptera: Lestidae). *Odonatologica* 7: 309-322.
- Fowler, J., L. Cohen & P. Jarvis, 1998: Practical statistics for field biology. Second edition. Wiley, Chichester.
- Hoess, R., 1993. Die aquatische Invertebratenfauna im Naturschutzgebiet Aured (Kleinbörsingen, FR). Lizentiatsarbeit, Zoologisches Institut Universität Bern.
- Jahn, A., 1991. Ökologische Untersuchungen über die Fauna einer Abbaugrube des Wendlands unter besonderer Berücksichtigung der Libellen. Staatsexamensarbeit, Universität Göttingen.
- Jödicke, R., 1997. Die Binsenjungfern und Winterlibellen Europas. Lestidae. Die Neue Brehm-Bücherei 631. Westarp, Magdeburg.
- Lawton, J.H., 1972. Sex ratios in Odonata larvae, with particular reference to the Zygoptera. *Odonatologica* 1: 209-219.
- Müller, O., 1995. Ökologische Untersuchungen an Gomphiden (Odonata: Gomphidae) unter besonderer Berücksichtigung ihrer Larvenstadien. Dissertation, Humboldt-Universität Berlin.
- Pajunen, V.I., 1962. Studies on the population ecology of *Leucorrhinia dubia* V.D. Lind. (Odon., Libellulidae). *Annales Zoologici Societatis Zoologicae-Botanicae Fennicae* (Vanamo) 24: 1-79.
- Pickup, J. & D.J. Thompson, 1984. The effects of prey density and temperature on development of larvae of the damselfly *Lestes sponsa* (Hans.) (Zygoptera: Lestidae). *Advances in Odonatology* 2: 169-176.
- Thompson, D.J., 1989. A population study of the Azure Damselfly *Coenagrion puella* (L.) in northern England. *Journal of the British Dragonfly Society* 5: 17-22.
- Westermann, K., 2000. Die Eiablageplätze der Weidenjungfer (*Chalcolestes viridis*) in einem südbadischen Altrheingebiet. *Naturschutz am Südlichen Oberrhein* 3: 93-107.
- Westermann, K., 2002a. Die Abundanz schlüpfender Libellen in einem südbadischen Altrheingebiet. *Naturschutz am Südlichen Oberrhein* 3: 215-244.
- Westermann, K., 2002b. Phänologie der Emergenz bei der Gemeinen Weidenjungfer (*Chalcolestes viridis*) an südbadischen Altrheinen. *Naturschutz am Südlichen Oberrhein* 3: 201-214.
- Westermann, K., 2003. Zum Schlüpfsubstrat der Gebänderten Prachtlibelle (*Calopteryx splendens*) an südbadischen Altrheinen. *Naturschutz am Südlichen Oberrhein* 4: 95-98.
- Westermann, K., 2006. Strategien frisch geschlüpfter *Lestes viridis* zur Vermeidung von Regenschäden (Odonata: Lestidae). *Libellula* 25: 47-60.
- Westermann, K. & S. Westermann, 1998. Die Quellgewässer und ihre Vegetation in der südbadischen Oberrheinniederung. *Naturschutz am Südlichen Oberrhein* 2: 1-93.